REVIEW: QUANTIFYING ANIMAL FEEDING BEHAVIOUR WITH A FOCUS ON PIGS

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Highlights:

- Feeding behaviour can be influenced by multiple factors.
- Several sensors exist to measure feeding behaviour in group-housed pigs.
- Units of feeding behaviour can be feeding visits, meals or raw registrations.
- Numerous methods for meal determination exist, with interesting recent advances.

1. ABSTRACT

The study of animal feeding behaviour is of interest to understand feeding, to investigate the effect of treatments and conditions or to predict illness. This paper reviews the different steps to undertake when studying animal feeding behaviour, with illustrations for group-housed pigs. First, one must be aware of the mechanisms that control feeding and the various influences that can change feeding behaviour. Satiety is shown to largely influence free feeding (*ad libitum* and without an operant condition) in animals, but 'free' feeding seems a very fragile process, given the many factors that can influence feeding behaviour. Second, a measurement method must be chosen that is compatible with the goal of the research. Several measurement methods exist, which lead to different experimental set-ups and measurement data. Sensors are available for lab conditions, for research on group-housed pigs and also for on-farm use. Most of these methods result in a record of feeding visits. However, these feeding visits are often found to be clustered into meals. Thus, the third step is to choose which unit of feeding behaviour to use for analysis. Depending on the situation, either meals, feeding visits, other raw data, or a combination thereof can be suitable. Meals are more appropriate for analysing short-term feeding behaviour, but this may not be true for disease detection. Further research is therefore needed. To cluster visits into meals, an appropriate analysis method has to be selected. The last part of this paper provides a review and discussion of the existing methods for meal determination. A variety of methods exist, with the most recent methods based on the influence of satiety on feeding. More thorough validation of the recent methods, including validation from a behavioural point of view and uniformity in the applied methods is therefore necessary.

***Keywords*:** feeding behaviour, visit, meal, sensor, methodology, pig

2. INTRODUCTION

Feeding behaviour of animals has been studied extensively for more than 50 years. The reported studies aimed to understand feeding behaviour (1994), investigate the effects of treatments (Petrie and Gonyou, 1988), diets (Hyun et al., 1997) or housing conditions (Georgsson and Svendsen, 2002), or predict illness (Cornou et al., 2008). Different measuring methods have been used depending on the species and study, resulting in different data available for analysis. Observations of feeding behaviour were typically clustered into meals and therefore the gathered raw data were transformed to 'meal' data to perform further analysis. However, no unique criterion for defining a meal could be identified. Therefore, the state of the art on measuring feeding behaviour is critically reviewed for laboratory and farm animals with a focus on pigs. Emphasis is on the criteria to convert raw data into meals. Special attention is given to measurements of group-housed pigs and the recent advances in applying these systems on-farm.

First, a general introduction on feeding behaviour is given with a focus on the mechanisms of free feeding. Second, we give an overview of the methods that have been proposed for measuring feeding in pigs. The results of these measurements are 'feeding visits', defined based on the start and stop time of the visits to the feed trough and sometimes including the amount of feed taken. In the third section the different definitions of visits and meals (clustered visits) are discussed together with the advantages and disadvantages of these units of feeding. The last section presents a detailed discussion of the different methods that have been used to register meals.

3. BACKGROUND ON FEEDING BEHAVIOUR

3.1. UNDERSTANDING FEEDING MOTIVATION

Several researchers have investigated the patterns of spontaneous feeding to obtain insight into the mechanisms of feeding. Free feeding behaviour has been investigated in rats (Levitsky, 1974), zebra finches (Slater, 1974) monkeys (Natelson and Bonbright, 1978), pigs (Bigelow and Houpt, 1988), cows (Tolkamp et al., 2000) and many other species. The aim of these studies was often to propose a model for human physiology (Musial et al., 1999) or to establish the regulatory signals present in feeding (Davies, 1977). Davies (1977) reported that meal frequency was controlled by short-term regulatory signals in rats, while meal size was more regulated by long-term influences.

One of the main questions has been "Is feeding controlled by hunger, satiety or both?" This has been investigated by means of prandial correlations, the correlations between feeding and the intervals before or after feeding. Linking hunger and satiety with pre- or postprandial correlations has gotten mixed up in literature, however. Decastro (1981) stated that "… *the ad lib feeding rat regulated its intake on the basis of how much it had just eaten (satiety) rather than how long it had been since last feeding (hunger)*". Decastro (1981) thus relates satiety with the correlation between meal size and the subsequent between-feeding interval (postprandial correlation) and hunger with the correlation between meal size and the previous between-feeding interval (pre-prandial correlation). Savory (1981) and Tolkamp et al (2012) used the opposite hypothesis, however. To avoid confusion, we will use the hypothesis of Decastro throughout this study. Recently, the control of food intake has also been investigated by examining the probability of an animal starting and ending a meal versus the time since the last meal and the amount of feed consumed (Tolkamp et al., 2012).

When satiety controls feeding, a high correlation between meal size and postprandial interval (interval following the meal) can be expected. This has been reported in rats (Levitsky, 1974; Davies, 1977; Decastro, 1981), monkeys (Natelson and Bonbright, 1978), birds (Duncan et al., 1970; Slater, 1974; Tolkamp et al., 2012) and cows (Tolkamp et al., 2000). In other words, an animal will start feeding again when its satiety feeling is below a certain critical point. The time at which this occurs is correlated with the size of the previous meal. Clearance of the stomach and gastrointestinal tract and metabolic utilisation of the food were large determinants to this effect. However, (secondary) influences of quantity and quality of food and diurnal rhythms have also been reported (Davies, 1977; Lemagnen and Devos, 1980). Decastro (1981) showed that for rats, stomach energy content at the end of a meal had the strongest correlation with the following inter-meal interval, while meal size (or even meal duration) were very often used as (weak) measures for this energy content. Diurnal patterns in feeding could also be explained by satiety. For example, Kraly et al (1980) concluded that nocturnal feeding in rats was controlled by decreased satiety at nighttime versus daytime.

When hunger is the main control factor, animals are expected to regulate their meal size based on the time since the last feeding. A significant correlation between meal size and the pre-prandial interval (interval preceding the meal) was only found in specific situations, such as for very large inter-meal intervals in rats (Levitsky, 1974), for some zebra finches as a result of accidental encounters with the feed (Slater, 1974), and for broilers (Bokkers and Koene, 2003). Several authors

have suggested that meal offset is rather determined by feedback signals of stomach distension and caloric content of the meal (Lemagnen and Devos, 1980; Decastro, 1981).

The observations reported for pigs were quite different from those for the animals described above (often individually-housed laboratory animals). Bigelow and Houpt (1988) found no correlation between meal size and pre- or postprandial intervals in immature female pigs. Musial et al. (1999) also found no correlation between meal size and postprandial interval, but a moderate correlation between meal size and pre-prandial interval in mini-pigs housed in pairs. Young and Lawrence (1994) found that 60% of the group-housed growing-finishing pigs in their study showed no prandial correlation, 26% showed postprandial correlation, 10% showed pre-prandial correlation and the remaining 4% showed both types of regulation. Montgomery et al. (1978) found no important correlations in their pigs. These discrepancies are hypothesised to be due to the pigs' intrinsic need for routing and foraging (de Leeuw et al., 2008), synchronised feeding (Hsia and Woodgush, 1984) and the social constraints which force group-housed pigs to adapt their feeding behaviour (Young and Lawrence, 1994; Tolkamp et al., 2011a).

In summary, most animal studies agree that free feeding is mostly regulated by satiety (postprandial correlation) and that hunger mechanisms (pre-prandial correlation) only play a role in specific situations. An animal will start to feed when its satiety level is below a certain point, but in free feeding no build-up of hunger will occur. Meal size is regulated by short-term feedback signals of the gastrointestinal tract and not by the interval since the last meal (as would be when hunger is present). However, these conclusions were not confirmed by the studies in group-housed pigs. This suggests that feeding behaviour can be influenced by external factors. We discuss these factors in the following section.

3.2. EFFECTS ON FEEDING BEHAVIOUR

3.2.1. TREATMENTS AND DIETS

Various experimental setups have been used to establish not only the behavioural but also the physiological mechanisms in feeding. For example, normal rats have been compared to desalivated rats, rats recovering from lateral hypothalamic lesions (Kissilef, 1970), and hypothalamic, obese rats (Thomas and Mayer, 1978) to obtain insight in the regulatory mechanisms behind feeding behaviour and the occurrence of obesity.

In addition to animal treatments, food treatments can also have an effect (Forbes and Kyriazakis, 1995). Dietary fibre has been shown to prolong postprandial satiety, to increase welfare and to reduce stereotypic behaviours in pigs by reducing feeding motivation (de Leeuw et al., 2008). Increased lysine content in the pigs' diet changed feeding behaviour by reducing meal frequency and increasing meal size and duration (Hyun et al., 1997). Montgomery et al (1978) found a reduction in food intake and rate of eating as a result of amino acid deficiency in a pigs' diet. Many other examples of the effect of type or contents of feed on the feeding behaviour undoubtedly exist (for example Kanarek, 1976).

3.2.2. FEEDING AND HOUSING SYSTEM

The way food is presented to the animal has been shown to affect feeding behaviour. Restricting feed or an operant feeding condition changed feeding behaviour significantly in rats (Levitsky, 1974; Kanarek, 1976; Thomas and Mayer, 1978), monkeys (Natelson and Bonbright, 1978; Hansen et al., 1981) and pigs (Ingram and Legge, 1974). The relative roles of hunger and satiety can also be changed by operant conditions (Natelson and Bonbright, 1978; Hansen et al., 1981). The feeder design can have an effect in *ad libitum* feeding and can be optimised for performance and ease of feeding (Gonyou, 1999; Laitat et al., 2005). Nielsen et al (1996b) found that group-housed growing pigs fed from a four-space feeder ate more frequently, but stayed less time and ate smaller quantities than pigs fed from a single-space feeder. Gonyou and Lou (2000) found feeding behaviour differences between single-space and multi-space feeders and between dry and wet/dry feeder types. Availability of water in the feeder was reported to increase feed intake and daily gain and to decrease the eating time (Gonyou and Lou, 2000). Also an effect of the distribution of feeders (distance between them) on the feeding behaviour of pigs was found (Thomsen et al., 2010).

The housing system and social influences also significantly affect feeding behaviour (Georgsson and Svendsen, 2002). Group-housed pigs were reported to have fewer meals and a lower general intake, but they had a higher meal size, meal duration, and rate of feed intake than individually housed pigs (de Haer and de Vries, 1993b). Pigs housed in large groups with one single-space feeder (thus a high animal feed place ratio) reduced their frequency of feeding, but increased the eating speed, duration and intake per visit compared to pigs in smaller groups (Nielsen et al., 1995). Therefore, excessively high constraints on animal feed place ratio and social and aggressive interactions can decrease the performance of individual pigs, as they might not be able to maintain their desired daily intake. Habit also plays a role. Nielsen et al (1996a) reported that individually-housed pigs that were previously group-housed modified their feeding behaviour only slightly, just enough to compensate for the previous constraints.

3.2.3. HEALTH AND BREED

Several animal-based factors influence feeding behaviour. Illness has been associated with changes in feeding behaviour, especially in the early stages of disease development (Hart, 1988; Weary et al., 2009). This indicates that frequent measurement of feeding behaviour in farm animals could be a very useful tool for automated disease detection. Diseased cows were reported to spend significantly less time at the feeder than healthy cows (Sowell et al., 1998; Gonzalez et al., 2008). Cornou et al. (2008) proposed a method for detecting oestrus as well as lameness and other health disorders for group-housed sows using their individual eating rank. For growing-finishing pigs, disease detection based on the feeding behaviour shows promising results (Hessel and Van den Weghe, 2011; Brown-Brandl et al., 2013). Changes in feeding frequency in pigs might even predict outbreaks of tail biting (Wallenbeck and Keeling, 2013). Feeding behaviour can also be used as indicator for social constraints in group-housed animals (Nielsen, 1999). Breed is also a determining factor in feeding behaviour (de Haer and de Vries, 1993a; Bokkers and Koene, 2003; Fernandez et al., 2011). Genetic selection or breeding decisions can be based on desired feeding behaviour (de Haer et al., 1993; Hoy et al., 2012).

3.2.4. ENVIRONMENT

The environment also has an effect on animal behaviour. Forbes and Kyriazakis (1995) adequately described many influences on diet selection, which can also apply to feeding behaviour: sensory properties, learning and memory, social influences, external influences, etc. Synchronised feeding between individuals was found in pigs (Hsia and Woodgush, 1984; Nielsen et al., 1996b). Petrie and Gonyou (1988) were even able to stimulate feeding in newly weaned piglets using auditory stimuli. Environmental temperature has a large influence (Ingram and Legge, 1974; Quiniou et al., 2000; Eigenberg et al., 2002), as well as light schedule (Feddes et al., 1989), body weight and sex of the individual (Bruininx et al., 2001b; Hyun and Ellis, 2002). However, even when all these influences are kept constant, individual differences still exist (Hessel and Van den Weghe, 2011; Brown-Brandl et al., 2013).

The variety in results and influencing factors shows that animals can adopt very flexible feeding behaviour. Small differences in the conditions in which the animals live can affect the feeding behaviour and different animals have different ways of maintaining homeostasis. Care must be taken not to generalise results across species, experimental conditions and even individual animals, because feeding has long been shown to be a fragile and complex process (Kanarek, 1976; Savory, 1981).

4. MEASURING FEEDING BEHAVIOUR OF PIGS

In the following section, an overview is given of the different sensors used to measure feeding behaviour of pigs based on over 30 papers between 1978 and 2014. Feeding behaviour is the act of feeding which can be described by ‘chewing or biting food’ or ‘putting the head in the trough’, also called a feeding visit. The discussion in this review is limited to the latter, as chewing or biting are difficult to measure without interfering with the animal.

4.1. INDIVIDUALLY HOUSED PIGS

For individually housed pigs, several sensors have been used to measure feeding behaviour. Several of these are adaptations from commonly used laboratory techniques such as those used for rats. Identifying the feeding animal is not necessary in this situation, because detecting the presence of an animal or observing the disappearance of feed is sufficient.

Montgomery et al (1978) used individual metabolism crates. The weight of the feed bin was measured using a spring balance connected to a potentiometer and recorder. By registering the scale imbalance throughout time, durations of feed bouts and intervals between bouts could be measured. Eigenberg et al (2002) used computer-controlled solenoids to lock the lid of each feeder and open it for 45 min four times a day. Amounts and duration were also measured using load cells. Auffray and Marcilloux (1980; 1983) developed a system using a rotating disc containing separate meals. The disc was activated by two photoelectric cells located under (recording the start of feeding) and in front of the feed trough (recording the end of feeding). Operant feeding in which the pig has to press a panel or lever to access a small amount of feed is also a possibility (Bigelow and Houpt, 1988; Musial et al., 1999). By multiplying the number of reinforcements with the amount of food distributed per press, the consumption can be estimated. Detecting the presence of a pig can also be done using an

infrared light beam inside the feeder. When a pig puts its head inside the feeder, the light beam is blocked and a micro-light switch is turned off. These on-off readings can then be recorded (Hsia and Woodgush, 1984), but no information about meal size is present in this case. Daily food intake can, however, be determined by weighing the supplied food and residual food of each pig.

As these systems require that the pigs are housed individually, the relevance of the obtained results for the farm conditions is rather limited. Therefore, systems for registering the feeding behaviour of group-housed pigs have also been elaborated.

4.2. GROUP-HOUSED PIGS

Before individual feeding behaviour of group-housed pigs can be measured, the individual pig must be identified. This can be done by simply marking and observing the pigs (either live or via video-recordings) (Lou and Gonyou, 1997; Gonyou and Lou, 2000; Morrison et al., 2007). Recent developments make it possible to automate video analysis of marked pigs, which would be an alternative way to determine their feeding behaviour (Gregersen et al., 2013; Kashiha et al., 2013). However, no reports were found of applying this technique on-farm. Radio Frequency Identification (RFID) provides a good alternative to the time-consuming task of marking and observing pigs. In these systems, the pig is equipped with a data-carrying transponder and the feeder is equipped with an antenna or reader system. When a transponder comes close to the antenna, its unique code is registered by the antenna (Maselyne et al., 2014b).

4.2.1. ELECTRONIC FEEDING STATIONS

For sows, the electronic sow feeder used on practical farms can be a valuable tool for research (Cornou et al., 2008; Junge et al., 2013). An example of an electronic sow feeder (Nedap, Groenlo, the Netherlands) is shown in Figure 1. Many other types and suppliers exist. The sow can enter a full protective crate around the feeder. A Low Frequency (LF) RFID antenna identifies the sow's ear transponder when she places her head inside the feed trough. A limited and balanced diet is then supplied to the sow while the entrance gate stays locked. When the sow stops feeding, she can exit the feeder through the exit gate and the entrance gate will unlock to allow the next sow to enter. Normally, only the daily feed ration and the number of visits to eat this ration are tracked. In some systems the timing of the visits is also recorded.

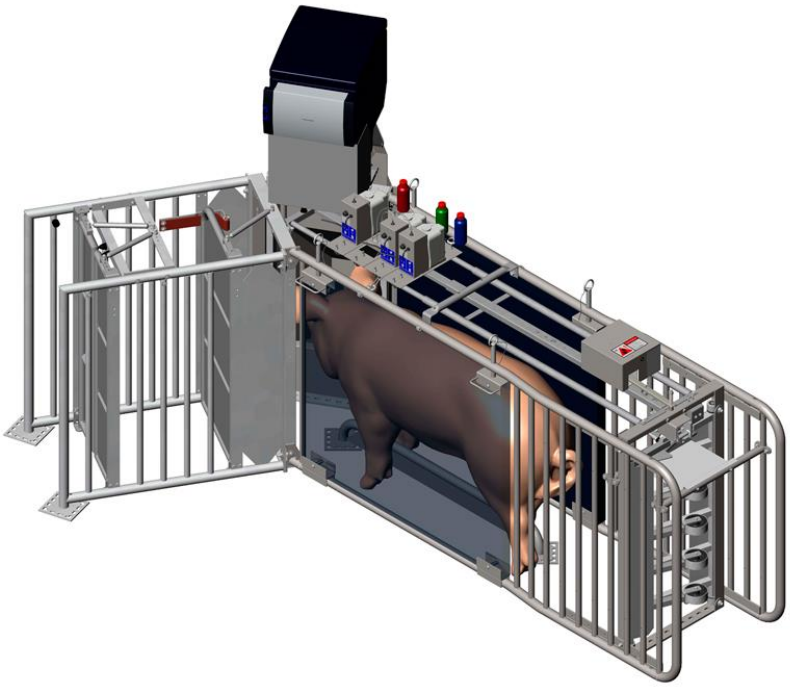

Figure 1: Electronic sow feeder (Nedap, Groenlo, the Netherlands), with entrance gate, protective crate, feed trough and exit gate (source: www.esf2013.com).

For growing-finishing pigs several similar devices exist (Wallenbeck and Keeling, 2013), although the electronic sow feeders could also be used directly for fattening pigs (Hoy et al., 2012). Slader and Gregory (1988) described an automatic feeding and weighing system; Quiniou et al (2000) described a single-space electronic feed dispenser. The most commonly used systems provide data recording of time and duration of each visit along with the weight of the food consumed. The F.I.R.E. (Feed Intake Recording Equipment, Osborne Industries, Inc., Osborne, Kansas USA) system illustrated in Figure 2a can be used as a stand-alone feeder or several types of protective crates can be added. The pigs have to push a door to access the feed. The electronic system records door opening; this is used as the start and stop of the feeding visits. Using RFID, the pig is identified and the trough is weighed before and after the feeding visit using a load cell. This type of system is currently used by several genetic companies and research groups (Nielsen et al., 1995; Nielsen et al., 1996a; Nielsen et al., 1996b; Hyun et al., 1997; Morgan et al., 2000a; Hyun and Ellis, 2002; Faltys et al., 2014). The IVOG (individual feed intake recording in group housing, Insentec B.V., Marknesse, the Netherlands) system is illustrated in Figure 2b. There is also a version for weanling piglets and a way to measure the animal's weight. The principle is the same: a dry single-space feeder placed on load cells with an adjustable fence that provides head and neck protection for the pig in front of the feeder. This fence also facilitates distinguishing feeding visits from each other. This system has been used in many studies (de Haer et al., 1993; de Haer and de Vries, 1993a; de Haer and de Vries, 1993b; Bruininx et al., 2001a; Bruininx et al., 2001b; Georgsson and Svendsen, 2002; Fernandez et al., 2011).

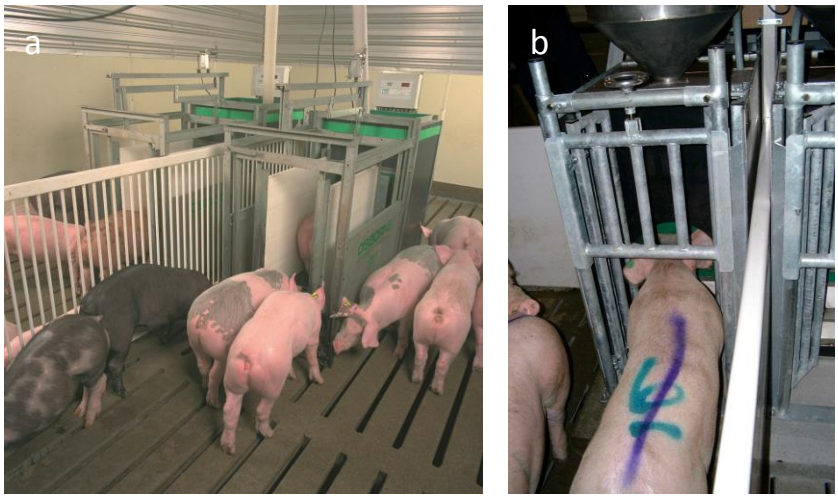

Figure 2: a) F.I.R.E. (Feed Intake Recording Equipment, Osborne Industries, Inc., Osborne, Kansas USA) with protective crate (source: www.osbornelivestockequipment.com); b) IVOG (individual feed intake recording in group housing, Insentec B.V., Marknesse, the Netherlands) for growing-finishing pigs (source: www.insentec.eu).

These electronic feeding stations have the advantage that the feed intake of each pig can be measured (ignoring possible spillage of food) and that identification of the single feeding pig is easy. However, due to the single feeding space and the protection the feeder provides for the pig, use of this system can change the feeding behaviour compared to normal farm conditions (with other types of feeders) (see section 3.2). This has its implications for research. Disadvantages are the need for frequent calibration and maintenance of load cells, supplying system for feed portions and other moving parts (Casey et al., 2005). Measurement errors can also occur and need to be dealt with properly (Casey et al., 2005). For sows, electronic feeders are used on-farm nowadays, but for growing-finishing pigs these systems lack adaptation on farm mainly due to the price and lack of useful applications (with the exception of genetic companies).

4.2.2. RFID SYSTEMS DEVELOPED FOR COMMERCIAL FEEDERS

Incorporating RFID antennas in feeders that are commonly used on commercial farms would allow feeding behaviour to be measured under farm conditions. Moreover, this could reduce the cost of the system compared to specially-designed feeding stations and increase the on-farm applicability of these systems (e.g. for illness detection).

A low-frequency (LF, 134.2 kHz) RFID system has recently been successfully integrated into a commercial multi-space rectangular feeder (Brown-Brandl and Eigenberg, 2011; Brown-Brandl et al., 2013). An LF RFID antenna was installed per feeding place (i.e. 5 antennas for the feeder in Figure 3a) and 30 antenna were connected to one microcontroller via a system of multiplexers. This resulted in readings taken with a 20 s scan time (each antenna was scanned every 20 s). Feeding visits were defined by consecutive readings for the same pig. In the previous systems, the start and stop of visits were defined by operands (gate opening) or extra sensors (food disappearance, light beam). Here, the RFID information itself was used. One antenna per feeding place was necessary, because LF systems cannot read multiple tags in range simultaneously. When more than one tag is in range of the antenna, data collisions occur and the data is lost.

To overcome this problem, RFID systems operating at higher frequencies (and with higher data transfer rates) incorporate anti-collision mechanisms. Maselyne et al (2014a) equipped a commercial round feeder with a High Frequency (HF, 13.56 MHz) antenna (Figure 3b). In this system, four antennas were connected to one reader using a multiplexer. Each antenna was scanned on average every 2 s. A smaller cycle time allowed for more accurate time measurements. Results have shown that readings of a feeding pig were not continuous when using this cycle time, because registrations can be 'missed' when transponders are momentarily out of range of the antenna due to their orientation (Maselyne et al., 2014b). To replicate visits, it then becomes necessary to cluster the RFID registrations (Mendes et al., 2011; Maselyne et al., 2014a).

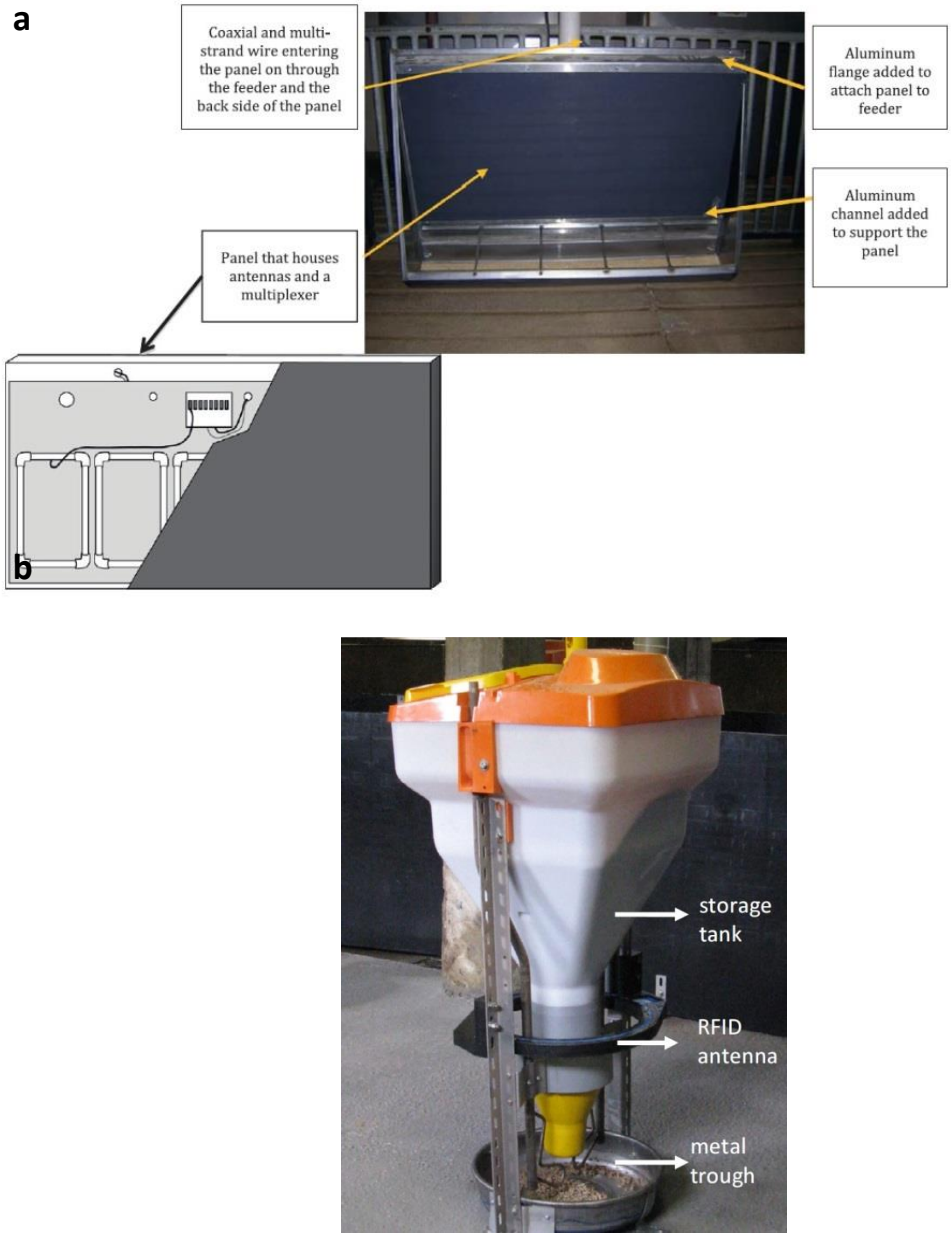

Figure 3: a) Low Frequency RFID system integrated in a commercial pig feeder (figure from Brown-Brandl et al., 2013); b) High Frequency RFID system integrated in a commercial feeder (figure from Maselyne et al., 2014a).

In summary, several systems are available to measure the feeding behaviour of pigs. For group-housed pigs, these systems mainly use Radio Frequency Identification (RFID) to identify the individual pigs. Most systems use specially-designed single-space feeders, resulting in clearly defined feeding visits and a record of the weight of the feed. The most recent advances are to incorporate RFID into commercially available feeders. This approach reduces costs and increases the potential for adoption by practical farms. However, the data collection and analysis can be more difficult. These different measuring methods result in different definitions of visits and different feeding behaviour, so one must choose the sensor best suited for the application by considering the advantages and limitations of the different systems. A thorough, detailed validation of the used system is also crucial to know the accuracy of the measured feeding patterns. An off-line measurement of the range of the RFID system *in situ* is necessary, since this range can vary depending on the type of materials in the area and the orientation and position of the tags (Maselyne et al., 2014b). Then, an online validation of the system has to be done to test whether it can discriminate feeding pigs from pigs that are not feeding (Maselyne et al., 2014a).

5. FEEDING OCCURS IN VISITS AND IN MEALS

In the previous section several methods for recording feeding visits of pigs have been discussed. However, feeding is usually not reported in terms of feeding visits, but rather in terms of meals. A meal is a cluster of feeding visits interrupted by short pauses. Although such meals have been observed in many species, obscurities still exist in the definition of a meal, its occurrence and the usefulness of the meal as a unit of analysis. Therefore, this section is dedicated to the relevance of defining meals and the different approaches which can be followed to define meals from the recorded feeding data.

5.1. UNITS OF FEEDING BEHAVIOUR

Variables used to describe feeding are bout size, interbout intervals, bout frequency, total food intake, rate of eating, bout duration, intake per bout, intake per large bout and so on (de Haer and de Vries, 1993b; Georgsson and Svendsen, 2002). Other related variables such as feeder occupation and daily weight gain are also sometimes mentioned (Hyun and Ellis, 2002). For species with a clear circadian rhythm, such as pigs (Montgomery et al., 1978; Hyun and Ellis, 2002), these variables are expressed in daily numbers or averages. In these variables a 'bout' can be either a 'feeding visit' or a 'meal'. This choice can have a large effect on the outcome of the studies (Tolkamp et al., 2000). It therefore deserves more attention.

Nielsen (1999) describes the inter-relatedness of feeding behaviour variables. The three main measures of feeding behaviour are number of meals per day, meal size and meal duration. Daily food intake, daily feeding time and feeding rate can be calculated through various combinations of two of these measures, but the reverse is not possible. Nielsen (1999) stated that an animal will try to maintain its daily food intake and has a preferred rate of feeding, assuming that these two measures are the most important for an animal. Notice that these two important measures (daily intake and feeding rate) are independent of the choice of 'feeding visits' or 'meals', but they do require that the intake is measured. Nielsen (1999) calculated the rate of feeding from the average meal size and average meal duration. However, an intra-meal variation in rate of intake can exist, as shown for goats (Giger-Reverdin et al., 2012). The statement of Nielsen (1999) is supported by findings that the

feeding rate of pigs stayed constant under different diets, levels of competition (although the feed intake differed) and ambient temperature (Hyun et al., 1997; Quiniou et al., 2000; Georgsson and Svendsen, 2002). Hyun and Ellis (2002) and Nielsen et al (1995), however, found a different feed consumption rate between pigs in different group sizes. de Haer and de Vries (1993b) also found similar differences between individually-housed and group-housed pigs; Nielsen (1999) states that this could be an indication of social stress. Most of these studies were with *ad libitum* fed animals (expect Georgsson and Svendsen (2002) which also had restricted feeding in their experiment) and with electronic feeding stations providing head and neck or full body protection, so it would be interesting to further investigate if feeding rate varies under other conditions.

Tolkamp et al (2000) established that meals are the biologically relevant unit for analysis of short-term feeding behaviour of cows. The probability of a cow ending a visit did not change with visit length, while the probability of ending and starting a meal did change with increasing meal length and inter-meal interval. The latter is what is expected if satiety plays a role. Therefore, meals are the correct unit when investigating prandial correlations. In addition, the visits seem to be largely affected by the animals' position in hierarchy, type of feeder and number of animals per feeding place (Tolkamp et al., 2000). Meal characteristics seem to be more stable, because the intra-group (or intra-treatment) variation in meals was much lower than the variation in visits (Tolkamp et al., 2000). Therefore, meals are more appropriate when investigating prandial correlations, occurrence of satiety and even differences between treatments for short-term feeding behaviour.

For detecting illness in cows, feeding time (sum of duration of feeding visits) was reported to be an important indicator (Sowell et al., 1998); it was even more important than feed intake, depending on the disease detected (Gonzalez et al., 2008). For goats, Giger-Reverdin et al (2012) showed that bouts of acidosis can be detected by segmenting and clustering the rate of feed intake without defining meals. In sows, individual eating rank can provide a basis for disease detection, but additional variables (such as daily intake or activity) are required to minimise false detections (Cornou et al., 2008). For growing-finishing pigs, pilot studies of disease detection through feeding behaviour were based on methods that did not provide a record of feed intake; these researchers assumed that feeding duration was an important measure (Hessel and Van den Weghe, 2011; Brown-Brandl et al., 2013). However, no detailed study exists that has evaluated the effectiveness of feeding visits versus meals for early disease detection in an individual. One might think that tracking meals is more relevant because meals will vary less in time compared to visits which are more affected by several factors (Tolkamp et al., 2000). However, one may not overlook that total visit time more closely reflects total feeding time. Further, the number of visits during a meal can indicate how often an animal is being chased away from the feeder and can thus indicate health or welfare problems. More research is thus needed on this topic.

Two important notes are necessary for this discussion. First, as mentioned above, the most recently-developed RFID systems for measuring feeding behaviour provide individual registrations or hits during a feeding visit without providing a clear beginning and end of the visit. The animal is allowed to eat freely in these systems and does not have to perform an extensive action to be able to feed (push open a door or enter a feeder crate). The gap between hits of a feeding animal can vary among systems (depending on the cycle time). One can assume that a feeding pig or cow is registered every cycle and define feeding visits in that manner (DeVries et al., 2003; Brown-Brandl and Eigenberg, 2011). However, a feeding pig is not always registered continuously, because the head movements

may hamper the tag detection by the antenna (Maselyne et al., 2014b). To replicate visits it is therefore necessary to cluster registrations (Mendes et al., 2011; Maselyne et al., 2014a). Either way, the raw RFID hits of these systems can also provide valuable information. DeVries et al (2003) showed that the repeatability within lactating cows is highest for the underived data, such as the number of hits per day (feeding activity) or the number of hits per meal minutes (feeding intensity). The repeatability of total daily mealtime, meal duration and meal frequency was only reported to be low to moderate.

Second, the transformation from raw data (RFID registration or feeding visits, depending on the system) to meals creates artefacts in the data. Several methods of meal determination exist (see section 6). However, it should already be noted here that these are all just approximations of the real underlying processes in the animal. Often one meal criterion is used for a group of animals or throughout time, but feeding differs between situations, individuals and age (see section 3.2). All these factors can create errors in the meal data, which creates the need to properly validate any meal model before using it.

When studying the short-term structure of feeding, meals are an appropriate measure. For disease detection, however, the feeding duration based on visits can suffice. The method of measurement also affects which measures are useful. For example, when no individual intake is measured, the two most important measures according to Nielsen (1999), i.e. daily intake and feeding rate, cannot be calculated. It is known that sows feeding from an electronic sow feeder often eat their entire ration in one visit, which makes it irrelevant to define meals (they have only one or two feeding visits per day) (Cornou et al., 2008). When individual hits (RFID registrations) are measured instead of visits, the raw data can be valuable as well. In short, the most relevant unit to define feeding behaviour depends on the situation.

5.2. MEAL CRITERION

Clustering feeding into meals has been observed in many species (Tolkamp et al., 2011b) and thus cannot be overlooked (Musial et al., 1999; Allcroft et al., 2004; Zorrilla et al., 2005). Feeding visits give a closer representation of the true feeding duration, while during a meal an animal is thought to be still 'busy with the concept of eating', even when it's not actually feeding. It is hypothesised that drinking can be part of a meal, but one can also think of social and especially aggressive interactions that can occur during pauses within a meal. The behavioural process underlying the concept of a meal is still unclear.

Concerning the definition of meals, these are generally based on mathematical considerations for clustering feeding visits. Feeding visits are clustered into meals using a meal criterion. A meal criterion is expressed in seconds or minutes and is the longest non-feeding interval still considered to be part of a meal or the minimum interval between visits to consider the next visit as part of a new meal (Howie et al., 2009; Tolkamp et al., 2011b). Notice the discrepancy in these two definitions. Often, the exact definition used for 'meal criterion' is not mentioned at all! The meal criterion is often pre-determined without reference to the motivation for this criterion (Kanarek, 1976; Thomas and Mayer, 1978; Brown-Brandl and Eigenberg, 2011; Mendes et al., 2011). In some studies the objective choice of a meal criterion was shown to be redundant, because it had no effect on the results (Levitsky, 1974; Montgomery et al., 1978). Other researchers tested a set of different criteria

to investigate how the results were affected (Kissilef, 1970; Decastro, 1981; Hansen et al., 1981). The use of visits in the analysis instead of meals has also been investigated (Gonyou and Lou, 2000; Georgsson and Svendsen, 2002). Auffray and Marcilloux (1980; 1983) stated that their pigs had meals which were well-separated without any pauses within the meal. They therefore did not define a meal criterion. More recently, several methods have been developed to determine meals objectively. These methods are the focus of the next section.

6. MEAL DETERMINATION

Table 1 lists the different methods used since 1970 to determine a meal criterion. Different methods of data representation have been used to visualise the feeding data during the process of meal determination (Table 1, first column). For each method of data representation, different methods for determining the meal criterion (defined as either the longest within-meal interval or the shortest between-meal interval) were also used. Sometimes a different criterion was used for every individual animal, while in other cases the criterion was deduced from and applied to the data of a group of animals. This results in a wide range of different meal criteria. For pigs, meal criteria between 30 s and 47 min have been used. Apart from feeding, these methods are also applicable to other clustered behaviours (Rook and Huckle, 1997) such as drinking (Clifton, 1987; Petrie and Gonyou, 1988; Musial et al., 1999) and lying down (Petrie and Gonyou, 1988; Tolkamp et al., 2010).

Method of data representation	Method of determining meal criterion	Papers	Animals	Criterion found
Frequency distribution of inter-feeding intervals	Fit negative exponential law while ignoring small intervals	(Duncan et al., 1970)	Chicken	2 min
	Least frequent interval	(Kissilef, 1970)	Rats	10 – 20 min
		(Kraly et al., 1980)	Rats	8 min
		(Lemagnen and Devos, 1980)	Rats	40 min
	Visual breakpoint	(Natelson and Bonbright, 1978)	Monkeys	5 or 20 min
		(Demaria-Pesce and Nicolaidis, 1998)	Rats	14 min
		(Petrie and Gonyou, 1988)	Piglets	7 min
	Two-slope broken line model	(Hyun et al., 1997)	Pigs	28.3 min
Log survivorship function	Visual breakpoint	(Slater, 1974)	Zebra finch	20, 40, 60 or 80 s, ~individual
		(Hsia and Woodgush, 1984)	Pigs	8.27 – 46.83 min, ~individual, ~weight
		(Bigelow and Houpt, 1988)	Pigs	10 min
		(Musial et al., 1999)	Miniature pigs	170 - 230 s, ~individual
	Negative exponential distributions	(Petrie and Gonyou, 1988)	Piglets	9 min
		(Tolkamp et al., 1998)	Cows	8.4 min
		(Tolkamp and Kyriazakis, 1999)	Cows	7.2 - 8.2 min, ~diet
		(Morgan et al., 2000b)	Pigs	30 min
		(Zorrilla et al., 2005)	Rats	18.6 or 120 s, ~method
		(Fernandez et al., 2011)	Pigs	~pig, average 30.01 s
Log frequency curve	2 or 3 negative exponentials	(Berdoy, 1993)	Rats	5.4 - 14.1 min, ~individual, method
		(Morgan et al., 2000a)	Pigs	1.2 min (2 exp.), 5.35 min (3 exp.)
Log transformed interval lengths	2 or 3 Gaussian models (log normal)	(Tolkamp et al., 1998)	Cows	38.3 min

Method of data representation	Method of determining meal criterion	Papers	Animals	Criterion found
		(Tolkamp and Kyriazakis, 1999)	Cows	32.3 - 38.3 min (2 log normal), 40.9 - 45.5 min (3 log normal), ~diet
		(Morgan et al., 2000a)	Pigs	1.29 min (2 log normal), 2.78 min (3 log normal)
	2 $\log_{10}$ frequency distributions	(DeVries et al., 2003)	Cows	27.74 min pooled, ~individual, time
	Mixed distribution models	(Yeates et al., 2001)	Cows	27.9 – 49.5 min, ~method
		(Howie et al., 2009)	Broilers	20.9 min
		(Howie et al., 2009)	Cows	28.9 min
		(Tolkamp et al., 2011b)	Cattle, pigs, chickens, ducks, turkeys, dolphins, rats	161 s – 30 min, ~species
		(Bailey et al., 2012)	Beef heifers	6.0 – 9.6 min, ~method
		(Zorrilla et al., 2005)	Rats	14 or 17.7 min, ~method
	Between-meal distribution	(Howie et al., 2009)	Broilers	20.1 min
		(Howie et al., 2009)	Cows	27.9 min
		(Howie et al., 2010)	Broilers, turkeys, ducks	1200 – 1725 s, ~species, hatch
Drinking-explicit method		(Zorrilla et al., 2005)	Rats	5 min
Analysis of starting probability		(Howie et al., 2009)	Broilers	17.5 min
		(Howie et al., 2009)	Cows	35.5 min
Behaviour studies	Resting as end of meal	(Kraly et al., 1980)	Rats	8 min
	Another behaviour as end of meal	(Bokkers and Koene, 2003)	Chicken	10 s
	Behavioural satiety sequence	(Zorrilla et al., 2005)	Rats	5 min

Table 1: Classification of methods to determine a meal criterion.

6.1. SUBJECTIVE METHODS AND METHODS ASSUMING RANDOMNESS IN FEEDING

One of the first methods developed relies on the frequency distribution of the intervals between feeding. This method builds on the observation that intervals during meals occur quite frequently, while the larger intervals between meals have a much smaller occurrence. Based on this observation, one could use a visual breakpoint in the histogram as meal criterion (Natelson and Bonbright, 1978; Petrie and Gonyou, 1988; Demaria-Pesce and Nicolaidis, 1998). The least frequent interval has also been used as meal criterion, with the underlying thought that satiety is maximal at that point and the probability of starting a new meal is minimal (Kissilef, 1970; Kraly et al., 1980; Lemagnen and Devos, 1980). Figure 4 shows two examples: Petrie and Gonyou (1988) for pigs and Lemagnen and Devos (1980) for rats. These methods are very subjective because visual observation of a breakpoint is not accurate and both methods depend on the choice of the bins in the histogram.

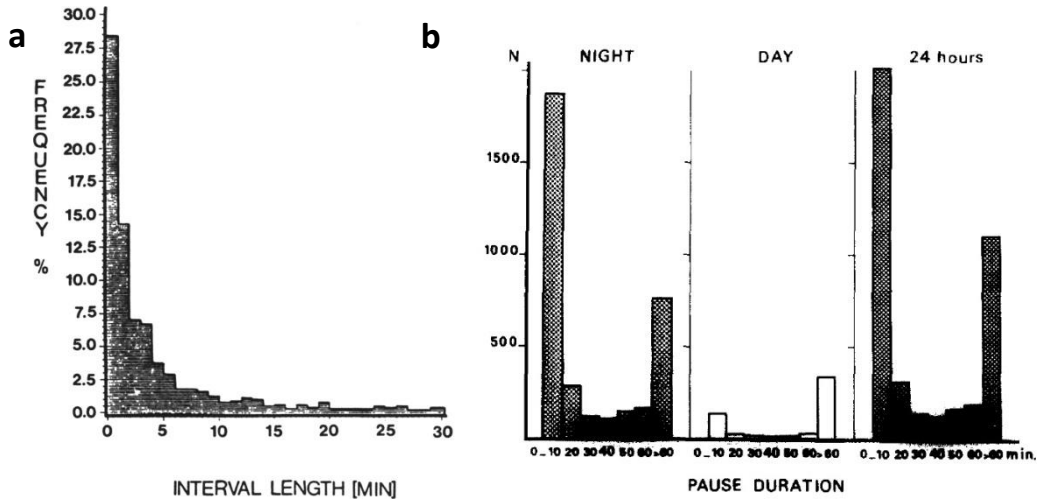

Figure 4: a) Frequency histogram of intervals between consecutive feedings of newly weaned piglets. Visual breakpoint was 7 min (figure from Petrie and Gonyou, 1988); b) Distribution of pause durations between feeding of rats. Least frequent interval was 40 min (figure from Lemagnen and Devos, 1980).

A more objective way to define the meal criterion is by fitting a negative exponential law to the frequency distribution:

$$f_{NE}(x) = e^{-x/\beta}/\beta \qquad (1)$$

with f_{NE} the probability density function and β the mean or expected value of the exponentially distributed variable *x*, in this case the length of intervals between feeding. In practice, using a histogram, the expected number of intervals between size a and b is then calculated as $N(e^{-a/\beta} - e^{-b/\beta})$, with *N* the total number of intervals (Duncan et al., 1970). Duncan et al (1970) considered the small intervals that had to be ignored for a good fit of the exponential law to be proof of the need to concentrate feeding into bouts. These small intervals were then considered the intervals within the meal. They applied this to birds and concluded that the exponential form of the distribution implicates that meals take place at random intervals (the interval lengths are independent from each other). Due to the negative exponential form of the distribution, a higher occurrence of smaller inter-meal interval lengths is assumed. A two-slope broken line model can also be fitted to the histogram to divide it into within- and between-meal intervals (Hyun et al., 1997). The broken line has two parts: a decreasing line $y = a + c(b - x)$ and a horizontal line $y = a$ with

the breakpoint *b* used as estimate for the meal criterion (Robbins et al., 1979). The broken line model thus assumes that all inter-meal interval lengths have the same frequency of occurrence.

Methods based on log survivorship analysis have been adopted more frequently. A log survivorship function is a backwards cumulative frequency distribution of the inter-feeding intervals on a logarithmic scale. A visual breakpoint in this curve is then used as a meal criterion (Slater, 1974; Hsia and Woodgush, 1984; Bigelow and Houpt, 1988; Musial et al., 1999). Figure 5a illustrates the example reported by Musial et al (1999). Clifton (1987) suggested fitting two overlapping negative exponential distributions to the log survivorship curve (thus two lines on the logarithmic scale), because this would allow then to calculate the breakpoint. The formula of the function fitted (after $\log_e$ transformation) to the log survivorship curve is then:

$$F_{LS}(X > x) = \alpha N e^{-x/\beta} + (1-\alpha) N e^{-x/\gamma} \qquad (2)$$

with $F_{LS}(X > x)$ the frequency of intervals with length $> x$ (so the backwards cumulative distribution function), β the expected value of the interval lengths between meals, γ the expected value of the interval lengths within meals, *N* the total number of intervals and α the portion of intervals between meals (Tolkamp et al., 1998). The meal criterion that assigns the least number of intervals to the wrong distribution is then equal to:

$$MC = \beta\gamma \, log_e((1-\alpha)\,\beta/\alpha\gamma)/(\beta-\gamma) \qquad (3)$$

(Tolkamp et al., 1998). This method gives similar results as the method of Duncan et al (1970), but gives a much better fit than using one negative exponential (Clifton, 1987). This method and variations upon have been applied in several studies (Petrie and Gonyou, 1988; Fernandez et al., 2011), see for example Figure 5b by Tolkamp et al (1998) for cows. Again, the assumption is that the probability of starting a new meal is independent of the time since the last meal (Tolkamp and Kyriazakis, 1999). This assumption has led this method to be contested in several studies. The log survivorship method was found to be insufficient for unpooled data of pigs (day and night data separately), for cows (Tolkamp et al., 1998; Tolkamp and Kyriazakis, 1999) and for rats (Zorrilla et al., 2005). The onset of meals does not follow a Poisson process, but was instead controlled by satiety, which would result in a convex log survivorship function between meals rather than a straight line (since there would be few very short and also few very long intervals between meals) (Tolkamp and Kyriazakis, 1999).

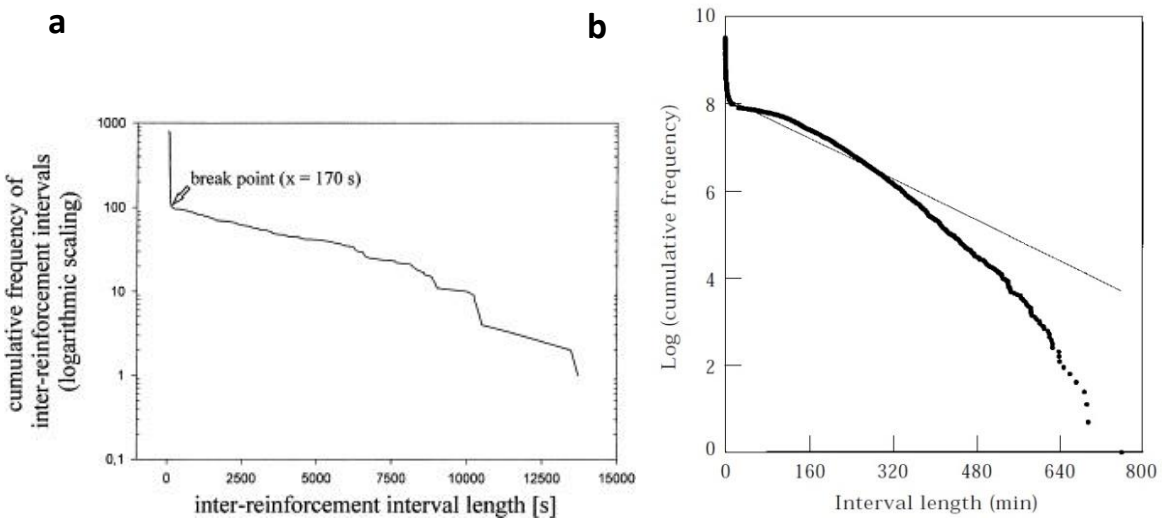

Figure 5: a) Log survivorship function of feeding of miniature pigs. Visual breakpoint was 170 s (figure from Musial et al., 1999); b) Log survivorship function of feeding of cattle with two negative exponential distributions fitted to it. Breakpoint between the 2 curves was 8.4 min (figure from Tolkamp et al., 1998).

Sibly et al (1990) stated that the points in a log survivorship plot are not independent and suggested using a log frequency plot (frequency distribution on a logarithmic scale) as a better representation. One or two negative exponentials could then be fitted to the plot and a bout criterion could be extracted. The model is then (after $\log_e$ transformation):

$$f_{LF}(x) = \alpha N e^{-x/\beta}/\beta + (1-\alpha) N e^{-x/\gamma}/\gamma \qquad (4)$$

with the same definitions and breakpoint (formula (3)) as before (Tolkamp et al., 1998). Berdoy (1993) and Morgan et al (2000a) stated that three random processes would give an even better fit. Such a log frequency curve for rats is illustrated in Figure 6 (Berdoy, 1993).

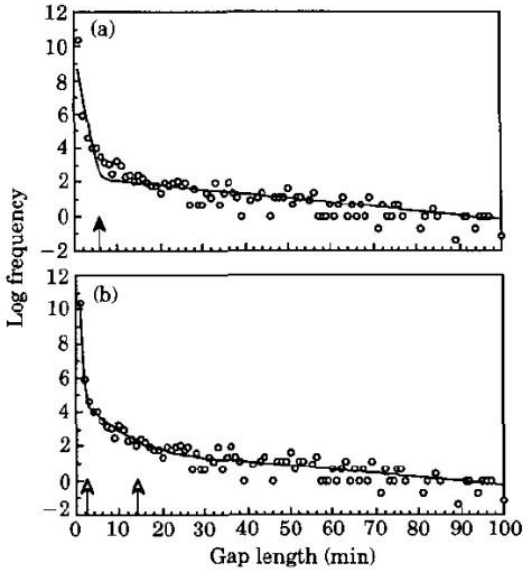

Figure 6: Log frequency curve of the gap length between feeding in rats (figure from Berdoy, 1993). Top plot is with two negative exponentials fitted to the curve; bottom plot is with three negative exponentials.

A major drawback of all these methods is that it is difficult to determine an objective criterion when the breakpoint in the curve is not clear. Almost all of these methods also build on the assumption that feeding is a Poisson process. It is therefore important to verify this assumption.

6.2. METHODS BASED ON SATIETY IN FEEDING

The assumption that feeding is a Poisson process contrasts with the satiety principle. One would expect that an animal is satiated after a meal, and the studies discussed in section 3.1 confirm this. This means that the probability of starting a new meal directly after the previous meal will be low and will increase with time, depending on the size of the meal that was just ingested (postprandial correlation) (Tolkamp et al., 2012). This makes the assumption of exponentially distributed interval lengths questionable, as both very short and very long inter-meal intervals become very unlikely (Tolkamp et al., 1998).

Tolkamp et al (1998) suggested examination of the frequency distribution of intervals in terms of the logarithm of the interval lengths (Figure 7). They came to this idea by inspecting the frequency distribution of the intervals between feeding of cows, which rather resembles a heavily skewed normal distribution. Taking the log transformation would normalise the data. After log transformation, two or three Gaussian curves could then be fitted to this curve (Tolkamp et al., 1998; Tolkamp and Kyriazakis, 1999) (Figure 7), with one Gaussian probability function being:

$$f_G(log_e(x)) = e^{-(log_e(x)-\mu)^2/2\sigma^2}/(\sigma\sqrt{2\pi}) \qquad (5)$$

with μ the mean and σ the standard deviation of the distribution (Tolkamp et al., 2011b). The fit of the three-curve model (so the sum of three Gaussian functions) was significantly better for cattle and pigs. The middle curve was considered to be a within-meal curve, which is often associated with drinking during meals (Tolkamp and Kyriazakis, 1999; Morgan et al., 2000a). In other studies the $\log_{10}$ transform of the interval lengths was used instead of the natural logarithm (DeVries et al., 2003). Care should be taken when interpreting the curves reported in literature as it is not always clearly specified whether the natural logarithm ($\log_e$) or the common logarithm ($\log_{10}$) has been used.

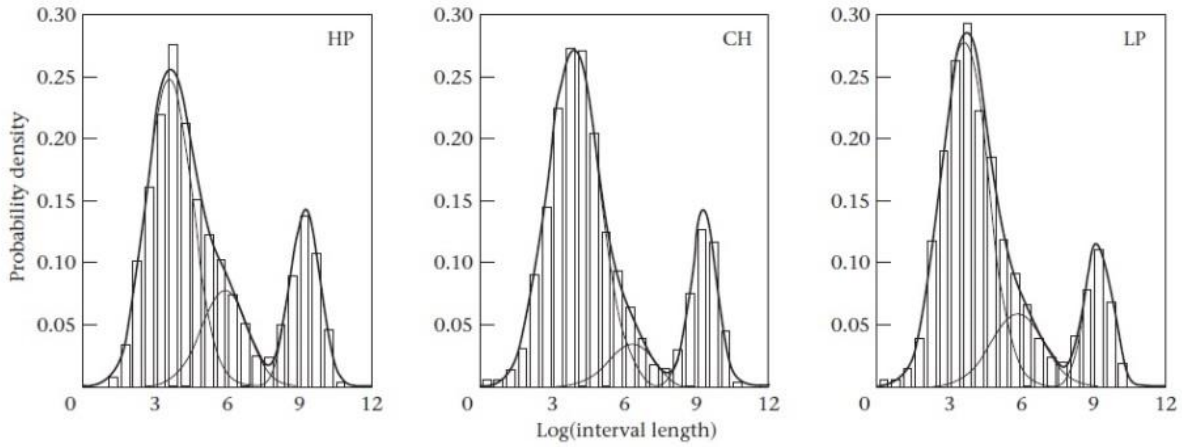

Figure 7: Probability density function with triple Gaussian model for log-transformed interval lengths of cows in dietary treatment with high protein (HP), choice between high and low protein (CH) and low protein (LP) (figure from Tolkamp and Kyriazakis, 1999).

Mixed distribution models have also been tested with Gaussian, Weibull:

$$f_W(log_e(x)) = c log_e(x)^{c-1}\, e^{-(log_e(x)/\alpha)^c}/\alpha^c \qquad (6)$$

(with α and c the scale and shape parameter) (Yeates et al., 2001), log-normal:

$$f_{LN}(log_e(x)) = e^{-(log_e(x)-\mu)^2/2\sigma^2}/(x\sigma\sqrt{2\pi}) \qquad (7)$$

Gamma:

$$f_{Ga}\big(log_e(x)\big) = log_e(x)^{k-1} e^{-log_e(x)/\theta}/(\theta^k \Gamma(k)) \qquad (8)$$

(with ϑ and k the scale and shape parameter and $\Gamma(k)$ the gamma function evaluated at k) and Gumbel distributions:

$$f_{Gu}\big(log_e(x)\big) = e^{-log_e(x)} e^{-e^{-log_e(x)}} \qquad (9)$$

to improve the fit on the $\log_e$ (Yeates et al., 2001; Zorrilla et al., 2005; Howie et al., 2009; Tolkamp et al., 2011b) or $\log_{10}$ transformed (Bailey et al., 2012) non-feeding intervals. A combination of Gaussian and Weibull distributions was found to give the best result for cows (Yeates et al., 2001; Bailey et al., 2012). For pooled data, a Gaussian distribution gave an excellent fit for the population of between-meal intervals. However, for individual animals or pooled data of animals with similar feeding strategies, the between-meal distribution is better described by a Weibull distribution. A Weibull distribution was found to be more accurate when describing the (increasing) probability of animals starting to feed since their last meal (Yeates et al., 2001; Tolkamp et al., 2011a).

Some of the recent methods described above have also been tested on pigs. However, the conclusions are not as straightforward as for cows. Morgan et al (2000a) tested both a 2- and 3-process random model on the log frequency plot and 2 or 3 Gaussian models on the distribution of log-transformed intervals. As in most other species, a 3-process model gave a better fit, which could be partially explained as drinking during a meal. Surprisingly, the random process model was found to give acceptable results. Morgan et al (2000b) found that this apparent randomness was due to incorrect pooling of data from the night and the day period. Tolkamp et al (2011b) found that feeding behaviour of the pigs in their study seemed random during the day, due to queuing at the feeder. Therefore, they fitted a truncated Gaussian and a Weibull distribution to the log-transformed intervals of the data at night only. For the data during the day, where the pigs were assumed to be unable to structure their feeding behaviour naturally, grouping the feeding behaviour into bouts was not considered to be useful (Tolkamp et al., 2011b).

In summary, these methods have been validated for several species and have clearly defined underlying assumptions that do not contradict the satiety principle. The suggestion to use a third distribution for the intervals related to drinking during the meal could be further validated by measuring drinking behaviour as well. This third distribution will depend, among other things, on the distance between the feeding and drinking device and the species. For example, Howie et al (2009) observed that broilers did not drink during meals. It should also be noted here that incorrect pooling of data can lead to faulty conclusions. Elaborate investigation of disaggregated data during meal determination is thus highly recommended.

6.3. OTHER METHODS

Some very promising alternative methods have been suggested recently. Zorrilla et al (2005) suggested a drinking-explicit method in which also the records of drinking behaviour were used to establish a meal criterion. They searched for the threshold interval between feeding and drinking records of rats which provided the most stable estimate of meal size and duration to minimise the consequences of incorrectly assigned events. Meal size and duration were estimated for a variety of threshold intervals and the local minimum in the first-derivative of this function was taken as the most robust criterion (Figure 8).

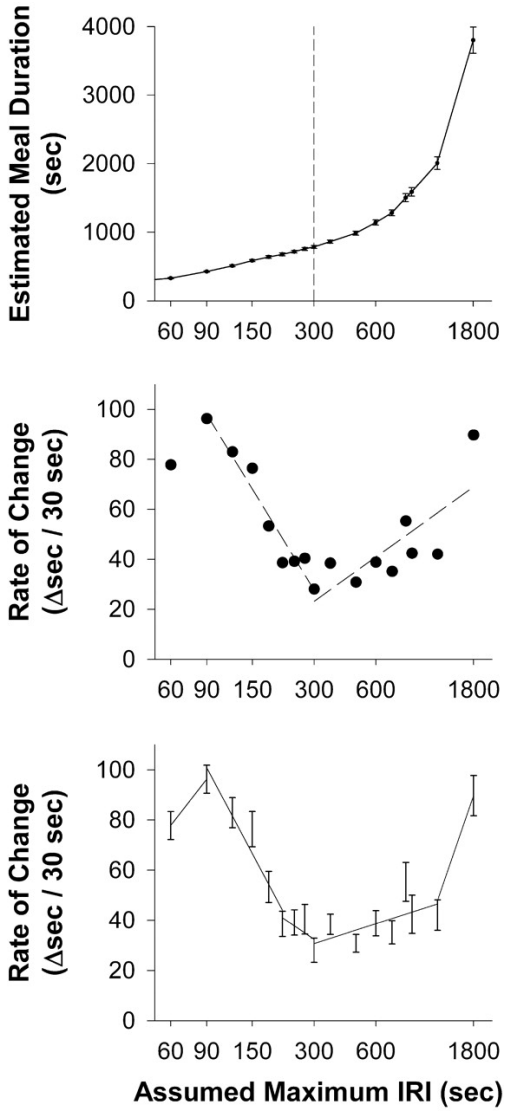

Figure 8: top: Estimated meal duration for several assumed maximum inter-registration intervals (intervals between panel-presses for feeding or drinking of rats); middle and bottom: first derivative with a two-segment linear regression or multivariate regression splines, respectively. Local minimum was estimated at 300 s (figure from Zorrilla et al., 2005).

Howie et al (2009) suggested that it might not be necessary to estimate the within-meal distribution(s) in the mixed distribution models of the log-transformed interval lengths discussed in section 6.2 to establish a meal criterion. Estimating the within-meal distribution(s) takes effort and

calculation time, while the correct distribution is not always clear. If one estimates the between-meal distribution only, the meal criterion can still be calculated as the interval length where the interval frequency is twice the frequency predicted by the between-meal interval distribution. Only an assumption of which intervals are too large to be part of a meal is necessary in advance. Howie et al (2009; 2010) reported that this method gave similar results as the mixed distribution models for birds and cows.

Another new and promising method is based on the analysis of the starting probability itself. This was tested on datasets of birds, rats, cows, dolphin calves and pigs (Howie et al., 2009; Howie et al., 2010; Tolkamp et al., 2011b). The probability of an animal starting feeding within the next minute (or another interval *k*) can be plotted versus the time since the last feeding:

$$P_{start}(t) = 1 - N_{\geq t+k}/N_{\geq t} = N_{\geq t \; and < t+k}/N_{\geq t} \qquad (10)$$

with *t* the time since the last meal, *k* the interval chosen and N_c the number of intervals that fulfil the condition *c* (Tolkamp et al., 2011b). This formula should be used when the meal criterion is defined as the smallest between-meal interval. When the meal criterion is defined as the largest within-meal interval, the formula should be (Howie et al., 2009):

$$P_{start}(t) = 1 - N_{>t+k}/N_{>t} = N_{>t \; and \leq t+k}/N_{>t} \qquad (11)$$

The meal criterion is then found at the point where the curve is minimal (Figure 9). When using this method, one must take care to not pool non-uniform data across feeding strategies, ages, etc. For example, the decrease in starting probability for large interval lengths in Figure 9 can be attributed to incorrect pooling. From the satiety concept, one would expect the starting probability to continue to increase; that is also the case when the data is disaggregated in uniform datasets (Howie et al., 2009).

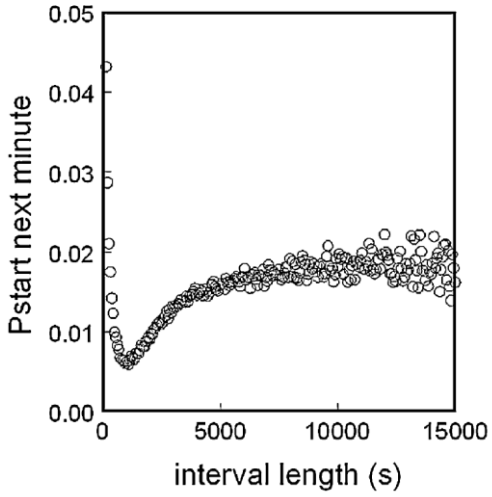

Figure 9: Starting probability of feeding during the next minute versus interval length between feeding for pooled data of broilers. Meal criterion is found in the minimum in the curve at 1050 s (figure from Howie et al., 2009).

The drinking-explicit method, the analysis of the distribution of between-meal interval lengths and the method using the starting probability can be applied in a straightforward fashion and would ease

the determination of meals compared to the 2 and 3–process models discussed above. Further validation of these techniques is necessary for other datasets, however.

The abovementioned methods define a meal based on statistical measures rather than behavioural measures. Kraly et al (1980) set the occurrence of resting as the criterion to identify the end of a meal for rats during daytime. Bokkers and Koene (2003) defined the end of a meal when birds performed another behaviour for 10 sec or more after feeding. Zorrilla et al (2005) performed a more detailed analysis of the behavioural satiety sequence in the 15 min following a meal under different candidate meal criteria. When doing so, the mathematically determined criteria were validated rather than determined. For example, resting increases after the meal, while drinking and activity decrease, suggesting a correctly defined meal (Figure 10). More work is needed on behavioural determination of meals. Indeed, meals should always be validated from a behavioural point of view. Solely statistical determination of meals does not guarantee that the meal definition is appropriate and biologically relevant. Because a meal is a cluster of feeding bouts in between which the animal is not satiated and thus still thinking about eating, its behaviour should reflect this state of mind.

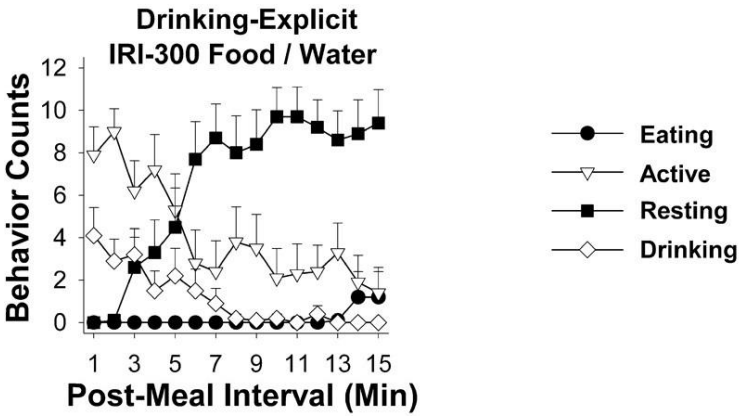

Figure 10: Behavioural satiety sequence for rats in the 15 min after a meal with the meal criterion determined via the drinking-explicit method (figure from Zorrilla et al., 2005).

To summarise, a wide variety of techniques for meal determination can be found in literature. The more recently developed methods build on the satiety principle, while older methods often assumed that feeding was random. Incorrect pooling of data can lead to faulty conclusions. It is therefore advisable to disaggregate data of individuals, different ages of the animals, treatments, etc. to see if the data is uniform or not. With the currently available methods it should be possible to define meals accurately, although most methods still require some extra validation. Especially the behavioural validation of meals should not be overlooked, because without a behavioural and physiological perspective of meals, assigning a 'meal' still remains an arbitrary choice. Answers to the questions 'What are meals?' and 'What happens during pauses within a meal?' remain partially unclear.

The large number of newly-developed methods calls for some uniformity in methods used. Nonetheless, a particular situation might require a different method. Howie et al (2009) pointed out that the methods they developed are able to estimate meal criteria independently from the effect on meal size and meal duration. This is in contrast to the method of Zorrilla et al (2005). It is disputable, however, whether this is an advantage or not. When analysing meal size and meal duration after meal determination (for example between treatments) one wants the most accurate estimate of

these measures rather that the correct classification of all between-feeding intervals. The latter can be more important for research into short-term feeding behaviour.

All methods require a large amount of data to estimate the meal criterion. Therefore, if one wants to estimate meals specific for herds, individuals or situations (which is definitely advisable), this can only happen after measuring the feeding. Online estimation of meals has not yet been elaborated. If meal criteria change with age and depend on the individual, online estimation of meals may become necessary for on-farm detection of illness based on meal variables. Despite the large number of studies dedicated to feeding behaviour and meal determination, further research is clearly still needed.

7. CONCLUSION

Feeding behaviour is mainly regulated by satiety mechanisms, as established by examining the prandial correlations in many species. But for pigs this is not always clear, possibly due to the large number of factors that influence the feeding behaviour of pigs. This review presents the different measurement methods designed to register feeding patterns of pigs. For group-housed pigs, RFID (Radio Frequency Identification) is a popular method for identifying a feeding pig. A meal is appropriate for investigating the structure of short-term feeding behaviour, but its appropriateness for other applications such as disease detection is not yet clear. Meal determination has received a great deal of attention and a variety of methods are available, but further work is still needed. Methods based on the satiety principle, prandial drinking, and the probability of starting a new feeding event are most promising. Incorrect pooling of data, drinking during meals, behavioural determination of meals and online estimation of meal criteria are some of the fields requiring further research.

Research on animal feeding behaviour should thus take the following four steps into consideration:

1. *Understanding feeding:* Feeding behaviour is controlled by mechanisms of hunger and satiety, but small circumstantial changes can drastically change an animal's feeding behaviour. Pigs' feeding behaviour can be influenced by treatments, diets, feeding and housing system, health, breed and environment. When designing an experiment or comparing studies, one must account for these influences.
2. *Choosing the sensor:* Several measurement methods for feeding behaviour of group-housed pigs have been proposed. Specially-designed feeding stations are available to measure feeding behaviour and intake, but some systems have recently become available that can be incorporated in commercial-type feeders for use in farm conditions. The appropriateness of the type of sensor depends on the experiment, but they all require proper validation.
3. *Choosing the appropriate unit:* Feeding behaviour can be expressed in terms of feeding visits or meals (clustered visits). Sometimes also other raw data is available, such as registrations of an animal. The appropriate unit depends on the goal of the research. Feeding visits reflect the feeding duration more closely, but meals can provide a more stable measure for feeding. Raw data has the advantage that it has not yet been manipulated, which avoids the possibility of errors due to data transformation.
4. *Choosing a method for meal determination:* Numerous methods for meal determination have been proposed. While some have been shown to be inaccurate or based on faulty underlying

principles, several new and promising methods have recently been reported. Here, the optimal method might also depend on the goal of the research. Note that incorrect pooling of data should be avoided and that behavioural validation of meals is necessary to guarantee an appropriate definition of the meal from a biological point of view.

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